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RESEARCH ARTICLE

Hydrodynamic function of dorsal fins in spiny dogfish and bamboo sharks during steady swimming

Anabela Maia[1,*,§], George V. Lauder[2] and Cheryl D. Wilga[1,‡]

ABSTRACT

A key feature of fish functional design is the presence of multiple fins that allow thrust vectoring and redirection of fluid momentum to contribute to both steady swimming and maneuvering. A number of previous studies have analyzed the function of dorsal fins in teleost fishes in this context, but the hydrodynamic function of dorsal fins in freely swimming sharks has not been analyzed, despite the potential for differential functional roles between the anterior and posterior dorsal fins. Previous anatomical research has suggested a primarily stabilizing role for shark dorsal fins. We evaluated the generality of this hypothesis by using time-resolved particle image velocimetry to record water flow patterns in the wake of both the anterior and posterior dorsal fins in two species of freely swimming sharks: bamboo sharks (*Chiloscyllium plagiosum*) and spiny dogfish (*Squalus acanthias*). Cross-correlation analysis of consecutive images was used to calculate stroke-averaged mean longitudinal and lateral velocity components, and vorticity. In spiny dogfish, we observed a velocity deficit in the wake of the first dorsal fin and flow acceleration behind the second dorsal fin, indicating that the first dorsal fin experiences net drag while the second dorsal fin can aid in propulsion. In contrast, the wake of both dorsal fins in bamboo sharks displayed increased net flow velocity in the majority of trials, reflecting a thrust contribution to steady swimming. In bamboo sharks, fluid flow in the wake of the second dorsal fin had higher absolute average velocity than that for first dorsal fin, and this may result from a positive vortex interaction between the first and second dorsal fins. These data suggest that the first dorsal fin in spiny dogfish has primarily a stabilizing function, while the second dorsal fin has a propulsive function. In bamboo sharks, both dorsal fins can contribute thrust and should be considered as propulsive adjuncts to the body during steady swimming. The function of shark dorsal fins can thus differ considerably among fins and species, and is not limited to a stabilizing role.

KEY WORDS: Elasmobranchs, Particle image velocimetry, PIV, Functional morphology, Locomotion, Wake, Flow visualization

INTRODUCTION

The dorsal fins of chondrichthyan fishes have a strikingly different muscular and skeletal arrangement compared with those in actinopterygian (ray-finned) fishes. The fin rays that support the fin in actinopterygian fishes are composed of two hemitrichia with muscles attached to each one (Alben et al., 2007; Geerlink and Videler, 1987). Contraction of muscles on one side causes the hemitrichs to slide past each other, putting the opposite side in tension, resulting in the bending of the fin ray towards the contracted muscle (Lauder, 2006). Although the musculoskeletal arrangement of fin supports in shark fins is less complex, with solid collagenous ceratotrichial fin rays that cannot generate active curvature, recent studies on the three-dimensional kinematics of the dorsal fin during steady swimming of spiny dogfish suggest a similar range of movement to that of dorsal fins in teleost fishes (Maia and Wilga, 2013a, 2016). This work indicates that the first dorsal fin of spiny dogfish can act as a stabilizer, moving independently of the trunk, while the second dorsal fin most likely functions as a thruster, moving with the trunk (Maia and Wilga, 2016). In bamboo sharks, both dorsal fins appear to act as thrusters during steady swimming based on three-dimensional kinematic data (Maia and Wilga, 2013b). During steady swimming, dorsal fin movements are not simply passively moved by fluid forces alone, but are also actively controlled by dorsal fin muscles (Maia and Wilga, 2013a). However, muscle activity and kinematic studies alone cannot provide direct evidence of thrust generation by dorsal fins. To investigate the effect of shark dorsal fin motion on fluid forces and to test the hypothesis that bamboo shark dorsal fins function differently from those of spiny dogfish, data on the fluid dynamics of shark dorsal fins are needed.

Particle image velocimetry (PIV) applied to freely swimming fishes (Müller et al., 1997; Drucker and Lauder, 1999) allows fluid flow around the body and fins to be visualized and quantified, and measurement of the lateral and thrust velocity components in the wake of moving fins provides a signature of thrust generation capability by fins. Studies of flow visualization have been applied to pectoral fins (Wilga and Lauder, 2000, 2001; Lauder et al., 2006), caudal fins (Lauder, 2000; Drucker and Lauder, 2000; Wilga and Lauder, 2004a; Tytell and Lauder, 2004), dorsal fins (Drucker and Lauder, 2001, 2005; Tytell, 2006; Standen and Lauder, 2007) and pelvic fins (Standen, 2010) in a diversity of fishes, but the hydrodynamic function of dual shark dorsal fins has not yet been analyzed.

Chiloscyllium plagiosum (Anonymous [Bennett] 1830, Order Orectolobiformes, Family Hemiscylliidae), white-spotted bamboo sharks, are a reef-dwelling species (Compagno, 1984). Bamboo sharks exhibit an anguilliform mode of locomotion during routine swimming (Compagno, 1984; Maia et al., 2012). Both the dorsal fins in bamboo sharks are placed on the posterior half of the body, closer to the tail than to the head, and the skeleton of the dorsal fins is composed of two rows of radials that span less than half of the fin area, with the rest of the fin web supported by ceratotrichia (Maia and Wilga, 2013b).

Squalus acanthias, Linnaeus 1758 (Order Squaliformes, Family Squalidae), the spiny or piked dogfish, inhabit coastal and

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continental shelf waters from temperate to subarctic regions (Compagno, 1984). *Squalus acanthias* can be found cruising near the bottom or in the water column, foraging on fish and squid (Compagno, 1984). Spiny dogfish have a large epicaudal lobe, lack anal fins, and swim using the body and caudal fin in an anguilliform mode of locomotion (Thomson and Simanek, 1977; Wilga and Lauder, 2004b). This species has two differently sized dorsal fins with an anteriorly located larger first dorsal fin and a second smaller dorsal fin close to the caudal peduncle (Maia and Wilga, 2016).

Ecological, anatomical and kinematic differences between the dorsal fins of bamboo sharks and spiny dogfish suggest that differences may exist in the hydrodynamic function of dorsal fins between these two species, and that further functional differentiation may occur between the anterior and posterior dorsal fins. Based on our previous kinematic and electromyographic work on shark dorsal fins, we hypothesized that (1) the hydrodynamic function of dorsal fins differs between bamboo and spiny dogfish shark species as a result of body shape, locomotor mode and fin placement, and more specifically that (2) anteriorly placed dorsal fins, i.e. the first dorsal fin of spiny dogfish, function as stabilizers because of their location near the center of mass, and (3) posteriorly placed dorsal fins, i.e. the second dorsal fin in spiny dogfish and both dorsal fins in bamboo sharks, generate thrust during steady swimming. We tested these hypotheses by analyzing longitudinal (along the shark axis) and lateral velocities and vorticity behind the dorsal fins. We expected thrust-enhancing fins to produce increased longitudinal velocities in relation to the incident flow to each fin, and vorticity resulting in a downstream-oriented fluid momentum jet. In contrast, we expected fins functioning as stabilizers to have decreasing longitudinal velocities, increasing lateral velocities, and vorticity resulting in laterally or anteriorly oriented fluid momentum jets.

MATERIALS AND METHODS

Experimental subjects

Four bamboo sharks, *Chiloscyllium plagiosum*, were shipped from Sea World, Orlando, FL, USA, and kept in a circular tank (1900 l) with 35 psu salinity, 22±1°C, on a 12 h light cycle and fed every other day on a natural diet of squid (*Illex* spp.) and fish (*Scomber* spp., *Clupea* spp., *Menidia* spp.). The total length of the individuals studied ranged from 39 to 45 cm. To rule out sex bias, two females and two males were used.

Four spiny dogfish, *Squalus acanthias*, were obtained from the Graduate School of Oceanography (URI) trawl. Individuals were kept in a circular tank (8900 l; 3 m diameter and 1.20 m tall). The tanks were maintained at 35 psu salinity, 18±1°C and on a 12 h light cycle. Sharks were fed every other day on a natural diet of fish (*Scomber* spp., *Clupea* spp.) and squid (*Illex* spp.). To rule out sex bias, two males and two females were used. The total length of the individuals studied ranged from 33 to 48 cm.

The experiments were approved under University of Rhode Island IACUC protocol no. AN05-07-001 and Harvard IACUC 20-03.

Experimental protocol

Sharks were placed in a flow tank and swam at either 0.75 body lengths (BL) s^{-1} or 1.0 BL s^{-1} in the 80 cm×26 cm×26 cm working area of a 600 l recirculating tank as in our previous research (e.g. Flammang and Lauder, 2009). One camera (Photron APX, Photron USA, San Diego, CA, USA) recorded the fish from above through a front surface mirror at a 45 deg angle (Fig. 1A). An optically clear plastic flat box with sides was placed on the surface above the fish to eliminate ripples and allow a clear view of the moving shark and dorsal fins. The camera was calibrated for all laser sheet positions with DaVis software (v7.2.2, LaVision GmbH, Göttingen, Germany) using an evenly spaced grid of points. This allowed compensation for spherical distortion introduced by the camera lens and mirror. Video was captured at 500 frames s^{-1} with a pixel resolution of 1024×1024. A Coherent I310 10 W argon-ion laser was used to illuminate neutrally buoyant 12 µm diameter plastic beads (density 1.3 g cm^{-3}; Potter Industries, Valley Forge, PA, USA). Cylindrical lenses were used to create a horizontal laser sheet that intersected the dorsal fins at approximately half the fin height (Fig. 1) when the sharks swam at the correct location in the flow tank. We were highly selective in choosing only sequences for analysis in which the dorsal fins intersected the light sheet at the mid-fin position. Fluid flow patterns were calculated from video recordings using standard multiple-pass PIV algorithms (Willert and Gharib, 1991) performed using DaVis software (v7.2.2, LaVision GmbH), which divides the image into a grid and performs cross-correlation within two consecutive frames to compute a matrix of velocity vectors, as in our previous research (e.g. Shelton et al., 2014; Nauwelaerts et al., 2007; Quinn et al., 2014).

Fluid flow analysis

Background fluid velocity was determined by manually identifying a small region in the free-stream flow well away from the influence of the shark body during swimming in the same video sequences (Fig. 1B). Flow variables in the wake of each fin were determined by identifying a region behind the fin that spanned the distance of the fin stroke. For the purpose of this study, fin stroke is defined as movement of the fin from maximum displacement of the trailing

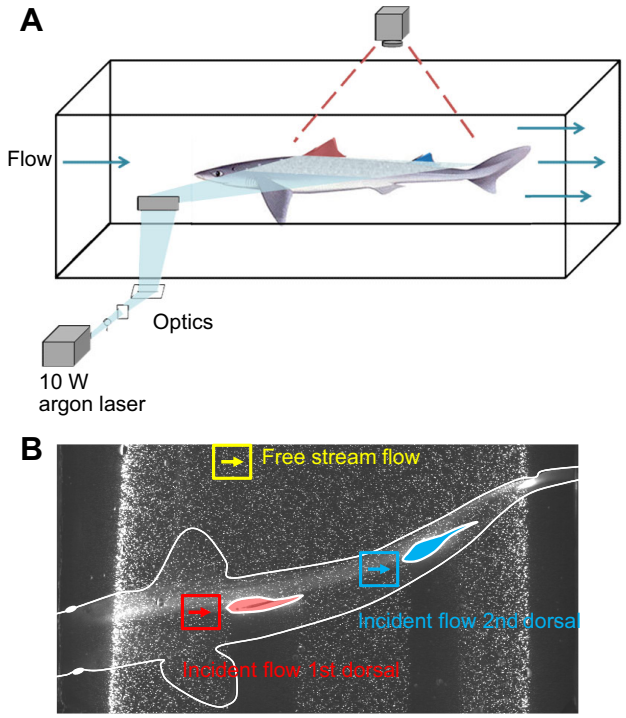

Fig. 1. Particle image velocimetry (PIV) experimental setup used to visualize fluid dynamics in the wake of the dorsal fins. (A) Schematic diagram of the experimental setup for flow visualization around the dorsal fins of freely swimming sharks. (B) Dorsal view image of the laser sheet being filmed for visualization of water flow over the fins and in their wake, including an explanation for free-stream flow and incident flow to each fin. The two dorsal fins are highlighted with the color code used throughout this paper: red for the first dorsal fin and blue for the second dorsal fin.

Journal of Experimental Biology (2017) 220, 3967-3975 doi:10.1242/jeb.152215

edge on one side to maximum displacement on the opposite side, i.e. between right and left maximum abduction. Incident fluid flow was determined upstream of each dorsal fin for each sequence analyzed using a similar size integration window to the one behind the fin (Fig. 1B). As lateral incident fluid flow was negligible, only the longitudinal velocity component was subtracted in the wake of each fin.

Mean stroke velocity in the longitudinal axis (v_x), i.e. along the fish axis, and the lateral axis (v_y) and vorticity were calculated for the area behind the fins. Mean variables are spatially and temporally integrated. Longitudinal and lateral components are indicators of forces contributing to thrust and stabilization, respectively (e.g. Drucker and Lauder, 2001; Standen and Lauder, 2007).

We would like to emphasize the rather considerable difficulty in getting individual sharks to swim with both the dorsal fins in a horizontal light sheet, and that relatively small differences in body position could contribute to data variability. Variation due to body height is exacerbated by the fact that sharks swim at the speeds studied here with a positive body angle to oncoming flow, so imaging both fins in the light sheet during free swimming is challenging. One effect of angled body position is that the light sheet is at slightly different heights away from the body behind each fin. We went to considerable lengths to only choose sequences where we felt that the light sheet for flow visualization was in the best possible position to capture undisturbed flows from both fins, but differences in relative light sheet height behind each fin may contribute to variation in flow fields because of these experimental challenges.

Statistical analyses

Two-way mixed model analysis of variance (ANOVA) was used to test for differences among individuals and speed for each species for velocity and vorticity variables. A three-way mixed model ANOVA was also used to test for differences in incident flow, with individual as a random effect and species and fins as fixed effects. Two-way mixed model ANOVA was used to test for differences in velocity and vorticity variables within each species using fins as fixed effects and individual as a random effect. A three-way mixed model ANOVA was used to test for differences in velocity and vorticity variables using species and fin as fixed effects and individual as a random effect. ANOVA analyses were conducted in R using the lme4 package for mixed models, and double-checked in SPSS. Tukey tests were used to test differences *a posteriori* (Zar, 2009).

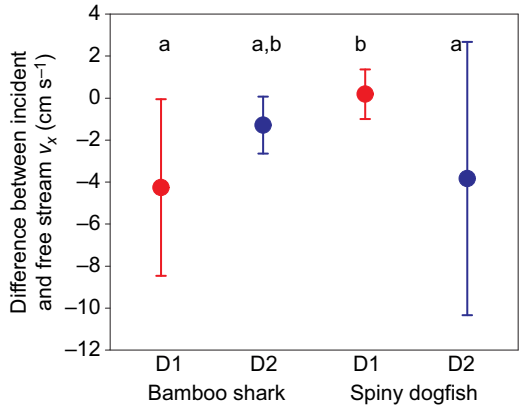

Fig. 2. Longitudinal incident flow to the dorsal fins is decelerated in the first dorsal fin of bamboo sharks and in the second dorsal fin of spiny dogfish relative to free-stream flow. Mean stroke-averaged longitudinal velocity (v_x) in front of each fin and away from the shark was subtracted for both species' first dorsal fin (D1) and second dorsal fin (D2). Circles represent the mean and error bars are standard deviation. Letters at the top of each panel denote fins and species that are significantly different from each other (see Results for more details). Bamboo shark N=4, spiny dogfish N=4.

RESULTS

Spiny dogfish

Data were collected for steady swimming in the water column at two different speeds. However, speed was not a significant predictor of dorsal fin wake velocity or vorticity (two-way ANOVA for all variables, P>0.05), and thus the data at 0.75 and 1.0 BL s^{-1} were combined for the remainder of the analyses.

We measured free-stream flow and incident flow (Fig. 1B) and noted that longitudinal incident flow was slowed down in relation to free-stream flow in the first dorsal fin of the bamboo shark and in the second dorsal fin of spiny dogfish (Fig. 2). We proceeded to correct the flow in the wake of each dorsal fin by the longitudinal incident flow to that fin to account for this deceleration caused by the postcranial region in bamboo sharks and the first dorsal fin in spiny dogfish. Instantaneous flow behind the dorsal fins showed deceleration behind the first dorsal fin (Fig. 3). Vorticity was present downstream of the second dorsal fin, but was not evident directly in the wake of the first dorsal fin. Longitudinal velocity profiles over a fin stroke were calculated 1 cm downstream from the dorsal fin trailing edge. For the first dorsal fin, flow was decelerated in relation

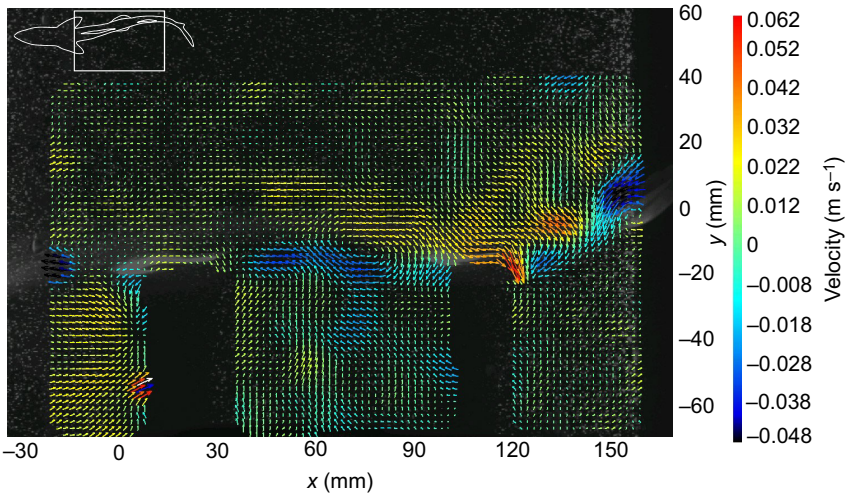

Fig. 3. Flow patterns behind the dorsal fins in a swimming spiny dogfish. Representative instantaneous velocity vector field around the dorsal fins of spiny dogfish when the first dorsal fin is at maximum abduction to the right and the second dorsal fin is at the end of the stroke to the left. Inset: the location of the analyzed region on the shark body. At this moment in time, there is a velocity decrement behind the first dorsal fin (note the blue vectors), and the second dorsal fin is accelerating flow (red vector colors), but, averaged over the entire fin stroke, flow is less than free-stream velocity for both fins (see Fig. 11A). A vortex can be seen in between the two dorsal fins. Mean free-stream flow has been subtracted.

Journal of Experimental Biology (2017) 220, 3967-3975 doi:10.1242/jeb.152215

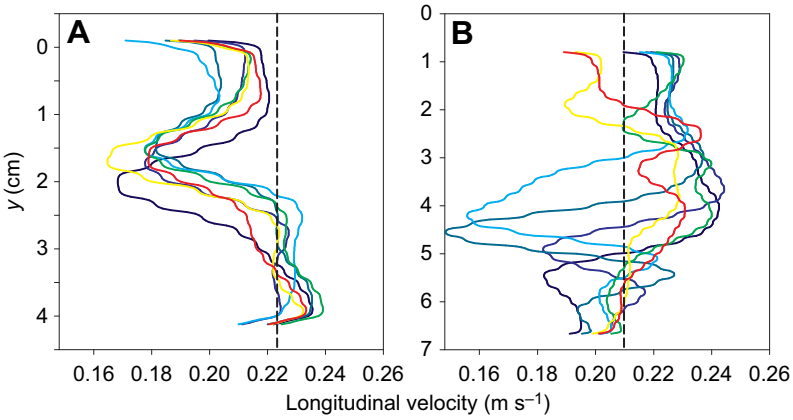

Fig. 4. Instantaneous longitudinal flow during the fin beat cycle in spiny dogfish. Instantaneous longitudinal flow is considerably decelerated behind the first dorsal fin (A) throughout a fin beat cycle and accelerated behind the second dorsal fin (B) shortly after the fin beat cycle begins. However, averaged over the entire fin stroke, flow is less than free-stream velocity behind the second dorsal fin (see Fig. 11A). Longitudinal velocity profiles were taken 1 cm downstream from the first (A) and second (B) dorsal fin during one fin stroke. Colored lines represent snapshots at 40 ms intervals; cooler colors represent the beginning of the stroke and warmer colors represent the end of the stroke. Mean dorsal fin position is centered on the *y*-axis. The dashed line represents incident longitudinal flow to each fin.

to incident flow (Fig. 4A), while for the second dorsal fin, flow was overall accelerated during the fin stroke (Fig. 4B; see also Fig. 11A).

Stroke-averaged velocity and vorticity showed a region of decelerated longitudinal flow behind the first dorsal fin, lateral velocity in the opposite direction to fin movement and an associated vorticity with a resulting jet towards the fin, i.e. zone of suction (Fig. 5). In contrast, the second dorsal fin showed increased longitudinal flow velocity in its wake accompanied by smaller lateral velocity components in the direction of the fin and the formation of vortices with a resulting jet pointing caudally (Fig. 6). When plotting the stroke-averaged variables over all trials and sharks, in over 90% of the trials the first dorsal fin decelerated flow, while the second dorsal fin accelerated flow, on average adding 4 cm s^{-1} to the incoming flow (see Fig. 11A). However, note the higher variation in longitudinal velocity for the second dorsal fin (see Fig. 11A). Overall, the mean longitudinal velocity was significantly higher for the second dorsal fin than for the first (Table 1, Fig. 11A). Mean lateral velocity and vorticity were not significantly different between dorsal fins, but were on average positive (Fig. 11B,C).

Bamboo sharks

Bamboo sharks had difficulty maintaining steady swimming high in the water column, so sequences of self-selected speeds near (within 1–2 cm) the bottom were gathered. Free-stream flow away from the shark was not different from that higher in the water column, indicating that we were well above the boundary layer. Instantaneous flow behind each dorsal fin was accelerated in relation to incident flow and vorticity was present downstream of both dorsal fins

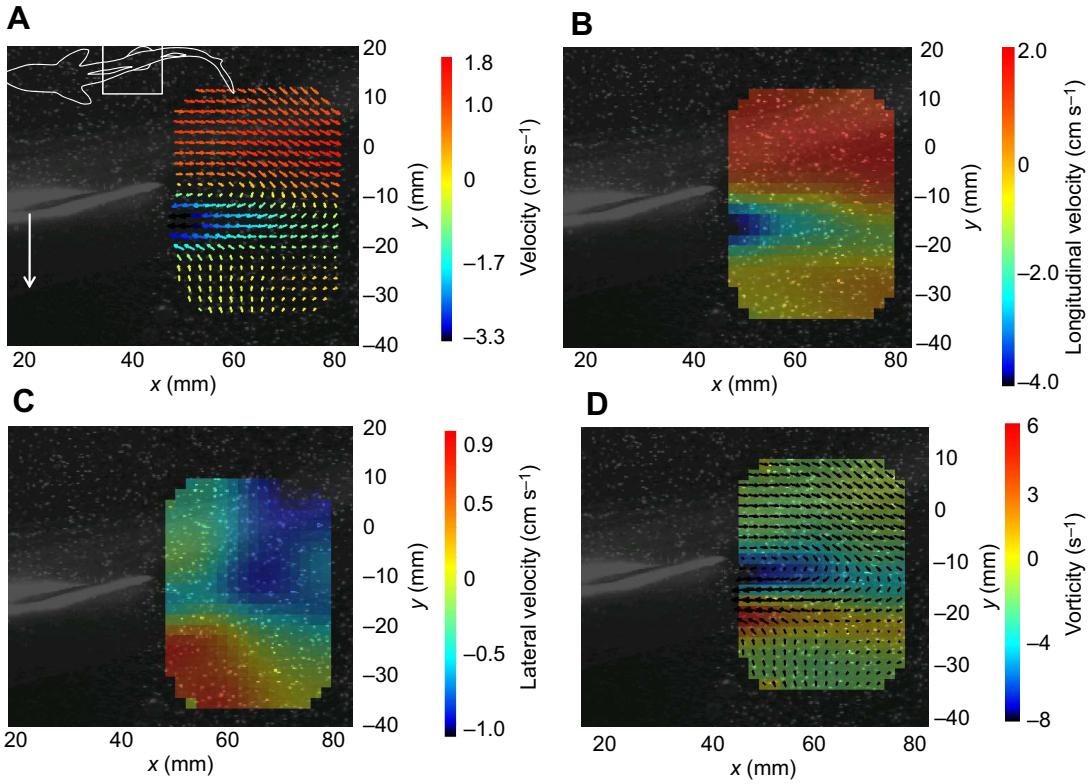

Fig. 5. Velocity, longitudinal velocity, lateral velocity and vorticity behind the first dorsal fin in spiny dogfish, showing flow deceleration. Stroke-averaged velocity and vorticity fields in the wake of the first dorsal fin in a spiny dogfish. (A) Velocity vector field. (B) Longitudinal velocity component. (C) Lateral velocity component. (D) Vorticity fields. Inset in A: the location of the analyzed region on the shark body. The shark image represents the position of the shark at the beginning of the analyzed sequence. Mean free-stream flow has been subtracted.

Journal of Experimental Biology (2017) 220, 3967-3975 doi:10.1242/jeb.152215

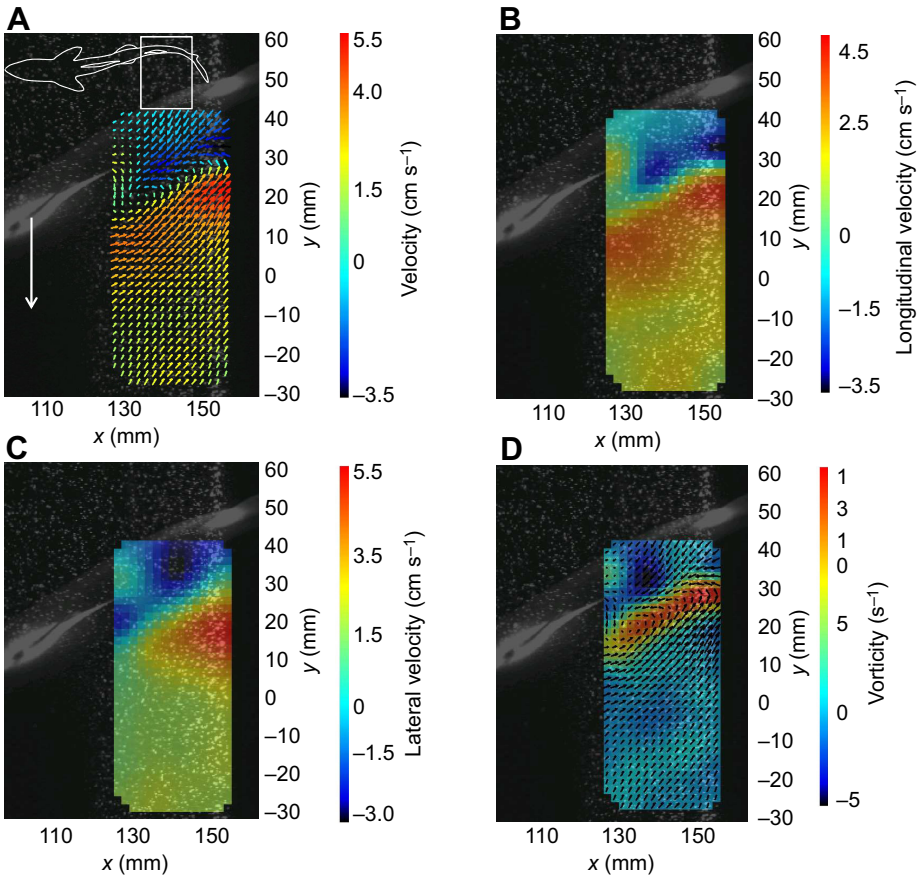

Fig. 6. Velocity, longitudinal velocity, lateral velocity and vorticity fields behind the second dorsal fin in spiny dogfish, showing flow acceleration. Stroke-averaged velocity and vorticity fields behind the wake of the second dorsal fin in a spiny dogfish. (A) Velocity vector field. (B) Longitudinal velocity component. (C) Lateral velocity component. (D) Vorticity fields. Averaged over the entire fin stroke, flow is less than free-stream velocity behind the second dorsal fin (see Fig. 11A). Inset in A: the location of the analyzed region on the shark body. Mean free-stream flow has been subtracted. The shark image represents the position of the shark at the beginning of the analyzed sequence.

(Fig. 7). Longitudinal velocity profiles over a fin stroke at a position 1 cm downstream from each dorsal fin showed acceleration of flow in relation to mean incident flow (Fig. 8).

Increases in stroke-averaged longitudinal velocity were detected behind the two dorsal fins, with a strong lateral component in the opposite direction to fin movement (Figs 9 and 10). Strong vortices were also detected behind both dorsal fins (Figs 9 and 10), and were higher for the first dorsal fin. When running two-way mixed model ANOVA with individual as a random effect and fin as a fixed effect, mean longitudinal velocity was similar between the dorsal fins (Fig. 11A). However, it should be noted that the first dorsal fin was more variable than the second. In contrast, mean lateral velocity was significantly higher behind the second dorsal fin (Fig. 11B), while vorticity was higher behind the first dorsal fin despite also having higher variability (Fig. 11C).

Comparison between species

Results from flow variables for spiny dogfish and bamboo sharks revealed differences in all variables tested between species as well as interactive effects between species and fins (three-way ANOVA, $P<0.05$, Fig. 11). Mean longitudinal velocity was different between fins and had interactive effects between species and fins (Fig. 11A). Mean lateral velocity differed between species and fins (Fig. 11B), while mean vorticity had differences between fins and species and had interactive effects between species and fins (Fig. 11B). Velocity and vorticity variables were generally higher for bamboo sharks than for spiny dogfish (Fig. 11). Also, there was a marked difference between the first dorsal fin in spiny dogfish, which is slowing down flow, and the second dorsal fin in spiny dogfish as well as both dorsal fins in bamboo sharks, which are overall accelerating flow (Fig. 11A).

Table 1. Velocity and vorticity variables for both dorsal fins in four individual sharks of each species during four trials of steady swimming at each speed

	Spiny dogfish		Bamboo shark	
	D1	D2	D1	D2
Mean v (cm s^{-1})	−1.19±2.50	0.71±7.76	0.45±5.16	1.87±3.08
Mean v_x (cm s^{-1})	−1.35±1.23	3.19±6.82	3.07±3.80	2.17±1.46
Mean v_y (cm s^{-1})	0.84±0.82	1.65±1.64	1±1.11	2.03±1.3
Vorticity (s^{-1})	0.65±0.61	0.93±1.19	2.56±1.73	1.24±0.65

Data are means±s.d., N=16. D1, first dorsal fin; D2, second dorsal fin; v, velocity in the longitudinal (x) and lateral (y) direction.

DISCUSSION

Dorsal fin fluid flow patterns

Our data show that the first and second dorsal fins of sharks have different hydrodynamic functions depending on the species. In spiny dogfish, the first dorsal fin decelerated flow 90% of the time and the second dorsal fin accelerated flow, while in bamboo sharks, both dorsal fins accelerated flow in the majority of the trials. Flow deceleration is likely related to a stabilizing function, while flow acceleration indicates thrust generation. Bamboo shark dorsal fins produce strong longitudinal velocity components with considerable lateral velocities that are higher for the second dorsal fin.

In spiny dogfish, large lateral velocities in the direction of fin movement in addition to reduced longitudinal flow velocity relative to incident flow in the wake of the first dorsal fin support the initial hypothesis that this fin is functioning as a stabilizer, as it is not generating thrust by adding streamwise momentum. This is to be expected as we have observed concurrent electromyographic activity in the left and right fin musculature (Maia and Wilga,

Journal of Experimental Biology (2017) 220, 3967-3975 doi:10.1242/jeb.152215

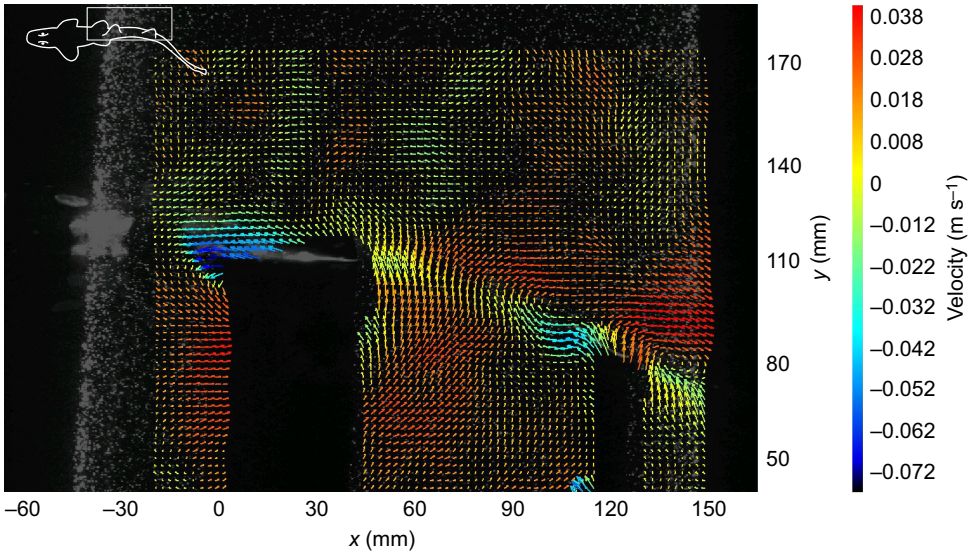

Fig. 7. Flow patterns behind the dorsal fins in a swimming bamboo shark. Representative instantaneous velocity field around bamboo shark dorsal fins when the first dorsal fin is at maximal abduction to the right and the second dorsal fin is half-way on a right-to-left stroke. Inset: the location of the analyzed region on the shark body. Mean free-stream flow has been subtracted.

2013b). Flow incident to the second dorsal fin is strongly decelerated in the wake of the first dorsal fin in relation to free-stream flow. A possible thrust function from this structure is supported by the instantaneous and stroke-averaged flow showing acceleration in the direction of fin movement (Figs 3 and 5), as well as by the peaks in instantaneous longitudinal velocity over a stroke (Fig. 4B). Previous work on this species has shown that the dorsal fin oscillates in phase with the body although it has higher lateral displacement than the body (Maia and Wilga, 2016). In addition, bilateral asynchronous muscle activity was observed, further corroborating that the second dorsal fin of spiny dogfish is not a passive structure (Maia and Wilga, 2013b). The second dorsal fin in spiny dogfish may function to reduce the effect of the wake velocity decrement generated by the first dorsal fin. The high variability among trials, especially in the longitudinal velocity behind the second dorsal fin, also deserves to be mentioned. It is possible that spiny dogfish are using the second dorsal fin for small corrections in heading during steady swimming. Further research into how this structure is used during maneuvers and while swimming in unsteady flows could shed some additional light on a stability role for this fin.

In bamboo sharks, the longitudinal component of velocity for the first dorsal fin was greater than incident flow but less than the free-stream flow, indicating that the postcranial region of the bamboo shark decelerates flow (Fig. 2). Body tilting during steady horizontal locomotion is common in sharks (Wilga and Lauder, 2000), and hence flow passing over the head and moving toward the first dorsal fin is likely to be decelerated relative to the free-stream flow before reaching the first dorsal fin. The high variability seen in the longitudinal velocity behind the fin might also be caused by the variable incident flow. The thrust component of the second dorsal fin is also higher than the incident flow. Strong longitudinal components in the wake of the dorsal fin are also present in bluegill sunfish during steady swimming (Drucker and Lauder, 2001; Tytell, 2006). In bluegill, the vortices shed in the wake of the dorsal fin interact and have additive effects to the tail vortices, which could also be happening for these two fins in sharks. Interactions with the tail are not likely in bamboo sharks because of a larger spacing between the second dorsal fin and the tail (Maia and Wilga, 2013b) and the subterminal shape of the tail's epicaudal lobe (Wilga and Lauder, 2004b). With this configuration, it is unlikely that the vortices shed at the second dorsal fin would encounter the vortices shed at the tail, and body tilting may place the tail at a more ventral position than the dorsal fins, allowing the fin wake to pass above the tail.

Lateral velocity components were present in the wake of both the first and second dorsal fin in both species. In general, the lateral velocity components were in the opposite direction to the moving fin, indicating that the water is moving from a high pressure region to a low pressure region, forming a jet in the opposite direction to fin

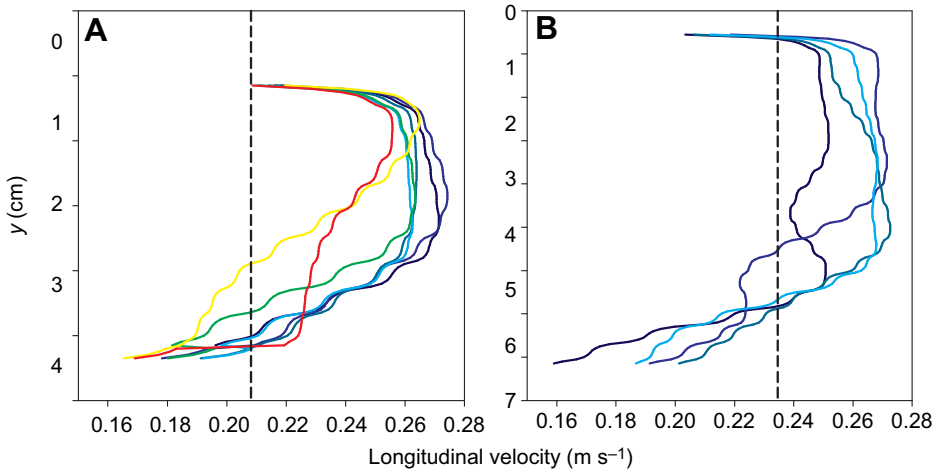

Fig. 8. Instantaneous longitudinal flow during the fin beat cycle in bamboo shark. Instantaneous longitudinal flow is accelerated in relation to free-stream flow behind the first (A) and second (B) dorsal fins throughout the fin beat cycle. Longitudinal velocity profiles were taken 1 cm posterior to the first (A) and second (B) dorsal fin during a single fin stroke. Colored lines represent snapshots at 40 ms intervals; cooler colors represent the beginning of the stroke and warmer colors represent the end of the stroke. The dashed line represents mean incident flow to each fin.

Journal of Experimental Biology (2017) 220, 3967-3975 doi:10.1242/jeb.152215

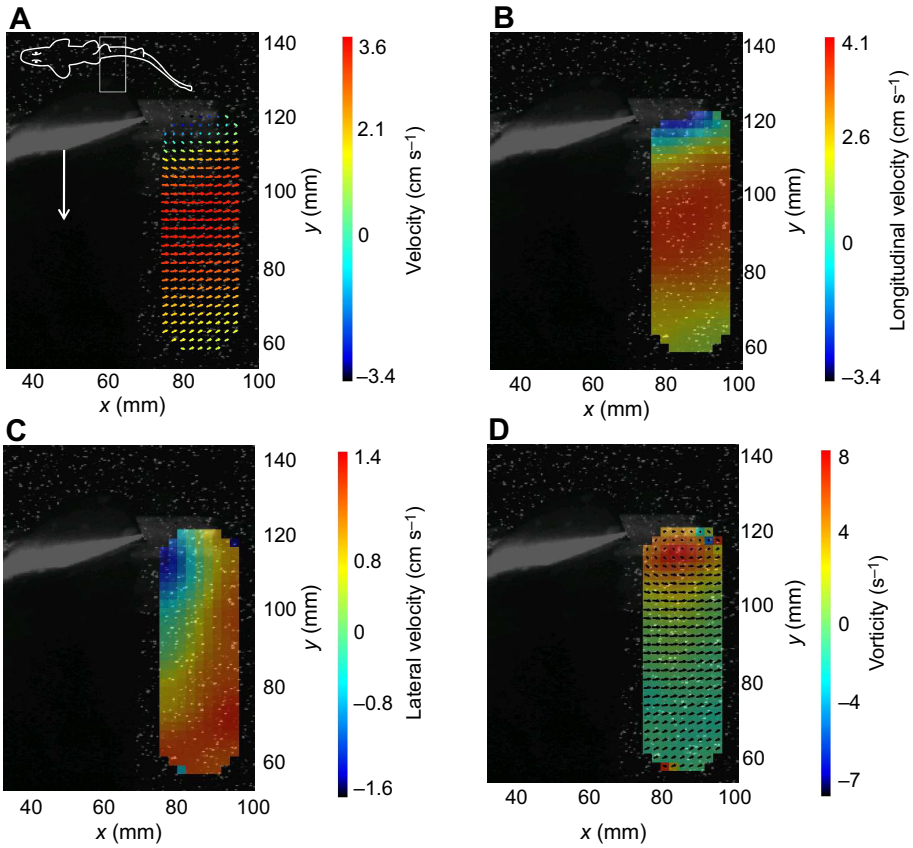

Fig. 9. Velocity, longitudinal velocity, lateral velocity and vorticity behind the first dorsal fin in bamboo sharks, showing flow acceleration. Stroke-averaged velocity and vorticity fields in the wake of the first dorsal fin in a bamboo shark. (A) Velocity vector field. (B) Longitudinal velocity component. (C) Lateral velocity component. (D) Vorticity fields. Inset in A: the location of the analyzed region on the shark body. The shark image represents the position of the shark at the beginning of the analyzed sequence.

movement. The only exception is the first dorsal fin in spiny dogfish, where the flow moves in the same direction as the fin. The first dorsal fin is relatively stiff (Maia and Wilga, 2013a) and the lack of fin bending during propulsion results in a different lateral velocity pattern and the lack of jet formation. In teleost fishes, fins functioning as active stabilizers beat laterally, producing large lateral forces, as shown by flow visualization data from the dorsal fin of brook trout (Standen and Lauder, 2007). In spiny dogfish, for the first dorsal fin,

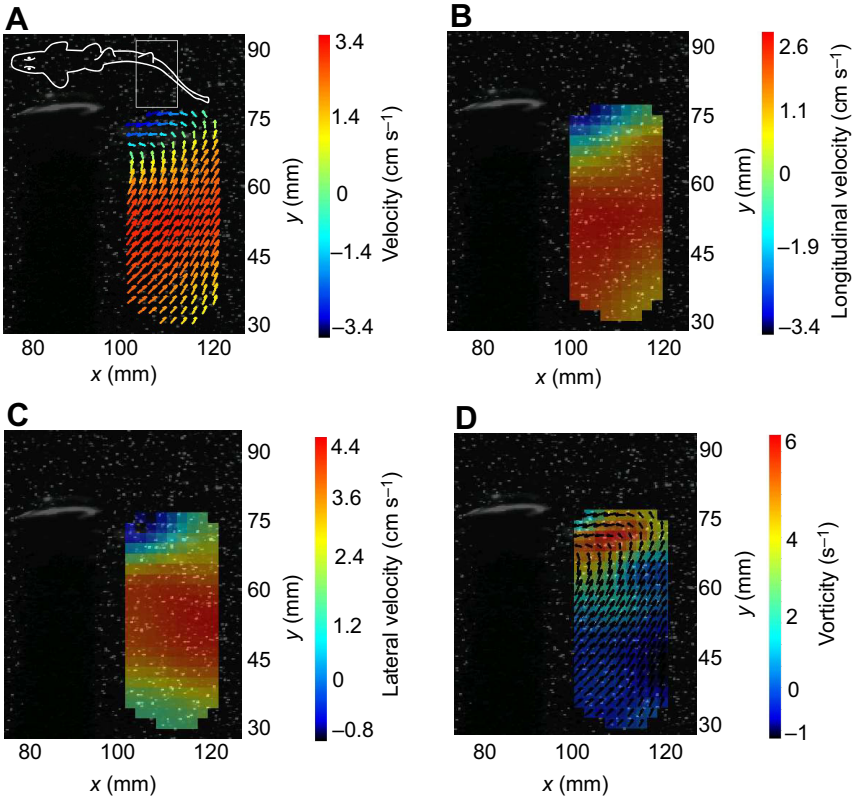

Fig. 10. Velocity, longitudinal velocity, lateral velocity and vorticity behind the second dorsal fin in bamboo sharks, showing flow acceleration. Stroke-averaged velocity and vorticity fields in the wake of the second dorsal fin in a bamboo shark. (A) Velocity vector field. (B) Longitudinal velocity component. (C) Lateral velocity component. (D) Vorticity fields. Inset in A: the location of the analyzed region on the shark body. The shark image represents the position of the shark at the beginning of the analyzed sequence.

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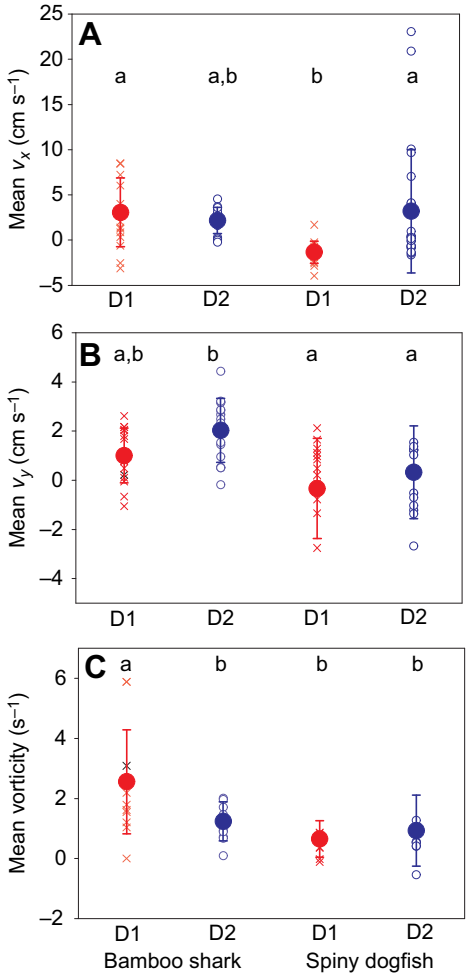

Fig. 11. Comparison of bamboo shark and spiny dogfish dorsal fin function. Mean stroke-averaged velocity and vorticity values for both species' first dorsal fin (D1) and second dorsal fin (D2). v_x, longitudinal velocity; v_y, lateral velocity (positive values represent displacement in the opposite direction to the fin stroke). Large circles represent the mean and error bars are standard deviation; circles and crosshairs represent individual trials. Letters at the top of each panel denote fins and species that are significantly different from each other (see Results for more details). Bamboo shark *N*=4, spiny dogfish *N*=4.

the lateral velocity component is not higher than the downstream (thrust) component, unlike the pattern observed in trout.

In bluegill sunfish, significant lateral velocities are present in the wake of thrust-producing fins, although the measured lateral component was lower than the thrust component (Drucker and Lauder, 2001). Lateral losses might be higher in sharks that use dorsal fins for propulsion when compared with actinopterygian fishes. This could stem from the lack of active control over individual fin ray curvature in sharks, in contrast to active fin curvature control observed in actinopterygian fishes (Standen and Lauder, 2005; Lauder, 2006). The relationship between supporting fin ray structures in fin, and patterns of hydrodynamic force generation is as yet not known, and represents an intriguing area for future study.

Mean stroke-averaged vorticity in the first dorsal fin of bamboo sharks was greater than that in the first dorsal fin of spiny dogfish, which is consistent with the larger area and larger muscle mass in bamboo shark dorsal fins and with larger lateral excursions (Maia and Wilga, 2013a,b, 2016). In bamboo sharks, mean vorticity shed by the first dorsal fin was double that of the second dorsal fin. Stronger vortices shed by the first dorsal fin suggest the possibility that in bamboo sharks there may be significant interactions between dorsal fin vortex structures. The motion of the second dorsal fin will occur in the wake shed by the first, and not in free-stream flow. Spiny dogfish mean vorticity was similar between fins. In general, spiny dogfish produced higher vorticity than bamboo sharks, although mean wake velocities were similar between the second dorsal fin of spiny dogfish and both dorsal fins in bamboo sharks. The presence of a spine in the anterior portion of the dorsal fin in spiny dogfish might limit creation of stronger wake vorticity as there is less muscle mass inserting into the ceratotrichia in the trailing edge and hence reduced amplitudes of kinematic oscillation. In contrast, bamboo sharks have relatively more massive musculature inserting into the dorsal fins and a skeletal arrangement that would favor trailing edge control to direct force (Maia and Wilga, 2013a).

Dorsal fin function

Traditionally, sharks were thought to have little control over fin shape and to use the dorsal fins passively to increase drag and deflect flow, allowing the dorsal fins to serve as stabilizers (Harris, 1936). This is partially true for the first dorsal fin of spiny dogfish, which we hypothesize functions as a stabilizer, resisting rolling torques on the body generated by caudal fin motion, although fin shape is actively controlled and resists hydrodynamic loads by bilateral muscle activation (Maia and Wilga, 2013a). However, a stabilizing function may incur locomotor costs as drag is increased and reduces downstream flow. A similar function of the dorsal fin for stabilization coupled to a slightly different behavior has been demonstrated in brook trout (Standen and Lauder, 2007).

In spiny dogfish, the second dorsal fin functions as a thruster, producing strong propulsive vortices and wake velocities above incident flow. Like the dorsal and anal fins in bluegill sunfish (Drucker and Lauder, 2001; Tytell, 2006), the vortices of the second dorsal fin in spiny dogfish appear to interact with the tail, although further research using three-dimensional vortex reconstruction (see Tytell, 2006) is necessary to fully demonstrate the extent to which three-dimensional vortices encounter the tail and modify flows generated there. In spiny dogfish, the tail vortices have been previously described as having a ring-within-a-ring vortex structure (see Flammang et al., 2011; Wilga and Lauder, 2004a). The complex shape of shark tail vortices may be due to the heterocercal shape, but could also be in part an effect of vorticity entrained from the wake of the second dorsal fin.

Bamboo sharks have more posteriorly placed dorsal fins, which beat actively to produce thrust (Maia and Wilga, 2013b; Fig. 11). The movement pattern of these fins and the distance between the fins suggest the possibility of an interaction between the two dorsal fins similar to the interaction between the dorsal fin and tail in bluegill sunfish (Drucker and Lauder, 2001). As incident flow was subtracted, the longitudinal velocity of the second dorsal fin is not larger than that of the first dorsal fin. However, incident flow at the second dorsal fin leading edge is higher than incident flow at the first dorsal fin leading edge, suggesting added momentum. The flow interaction in dorsal fins of bamboo sharks could be similar to the interaction modeled for flags in tandem (Alben, 2009). In order to produce maximal constructive vortical interactions, flags have to be synchronized with each other and placed at a specific distance (Alben, 2009). The distance between dorsal fins in bamboo and spiny dogfish sharks is fixed, which indicates that vortical interactions between fins may not occur all the time, and may depend in part on the magnitude and amplitude of upstream dorsal fin excursions, which are under active control.

An additional factor to consider in any discussion of fin–fin interactions has been highlighted by a computational study (Akhtar et al., 2007) using motion parameters of two fins in series, derived from experimental work on bluegill sunfish. It is not necessary for the upstream fin to produce a thrust wake in order to have a positive effect on thrust by the downstream fin. Even a narrow drag wake produced by an upstream fin with limited motion can induce early separation of the leading edge vortex on the downstream fin, and enhance thrust (Akhtar et al., 2007). Thrust increases on the downstream fin may occur by increasing leading edge suction, and this suggests a possible mechanism by which the spiny dogfish first dorsal fin, even though it does not generate thrust, could still improve the function of the second dorsal fin. Factors that might underlie the evolution of diverse dorsal fin external morphology, internal anatomy and stiffness, and function among shark species (Shirai, 1996; Wilga and Lauder, 2004b; Maia and Wilga, 2013a) are still unknown. There is considerable phylogenetic diversity among shark dorsal fins in position and stiffness, but kinematic and flow visualization analyses have only been accomplished for a few species that are amenable to laboratory investigation. Hydrodynamic effects of dorsal fin shape and position may depend in part on (1) fin location relative to the center of shark body mass, which will affect the magnitude of fin surface area effects in stabilizing roll torques without inducing yaw moments, (2) distance along the body to the tail, which will in part determine the strength and nature of vortical interactions, and (3) the distance between dorsal fins and the extent to which active oscillation occurs in each fin, which will determine the extent to which the dorsal fins contribute to thrust enhancement.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: A.M., G.V.L., C.A.W.; Methodology: A.M., G.V.L., C.A.W.; Validation: A.M., G.V.L.; Formal analysis: A.M., G.V.L.; Investigation: A.M., G.V.L., C.A.W.; Resources: A.M., G.V.L., C.A.W.; Data curation: A.M., G.V.L.; Writing - original draft: A.M., G.V.L., C.A.W.; Writing - review & editing: A.M., G.V.L., C.A.W.; Supervision: G.V.L., C.A.W.; Project administration: A.M., G.V.L., C.A.W.; Funding acquisition: A.M., G.V.L., C.A.W.

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References
Akhtar, I., Mittal, R., Lauder, G. V. and Drucker, E. (2007). Hydrodynamics of a biologically inspired tandem flapping foil configuration. *Theor. Comput. Fluid Dyn.* **21**, 155-170.
Alben, S. (2009). Wake-mediated synchronization and drafting in coupled flags. *J. Fluid Mech.* **641**, 489-496.
Alben, S., Madden, P. G. and Lauder, G. V. (2007). The mechanics of active fin-shape control in ray-finned fishes. *J. R. Soc. Interface* **4**, 243-256.
Compagno, L. J. V. (1984). *Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species known to Date*, Vol. 4. Rome: FAO Species Catalogue for Fishery Purposes.
Drucker, E. G. and Lauder, G. V. (1999). Locomotor forces on a swimming fish: three-dimensional vortex wake dynamics quantified using digital particle image velocimetry. *J. Exp. Biol.* **202**, 2393-2412.
Drucker, E. G. and Lauder, G. V. (2000). A hydrodynamic analysis of fish swimming speed: wake structure and locomotor force in slow and fast labriform swimmers. *J. Exp. Biol.* **203**, 2379-2393.
Drucker, E. G. and Lauder, G. V. (2001). Locomotor function of the dorsal fin in teleost fishes: experimental analysis of wake forces in sunfish. *J. Exp. Biol.* **204**, 2943-2958.
Drucker, E. G. and Lauder, G. V. (2005). Locomotor function of the dorsal fin in rainbow trout: kinematic patterns and hydrodynamic forces. *J. Exp. Biol.* **208**, 4479-4494.
Flammang, B. E. and Lauder, G. V. (2009). Caudal fin shape modulation and control during acceleration, braking and backing maneuvers in bluegill sunfish, *Lepomis macrochirus*. *J. Exp. Biol.* **212**, 277-286.
Flammang, B. E., Lauder, G. V., Troolin, D. R. and Strand, T. (2011). Volumetric imaging of shark tail hydrodynamics reveals a three-dimensional dual-ring vortex wake structure. *Proc. R. Soc. B* **278**, 3670-3678.
Geerlink, P. J. and Videler, J. J. (1987). The relation between structure and bending properties of teleost fin rays Neth. *J. Zool.* **37**, 59-80.
Harris, J. E. (1936). The role of the fins in the equilibrium of the swimming fish. II. The role of the pelvic fins. *J. Exp. Biol.* **15**, 32-47.
Lauder, G. V. (2000). Function of the caudal fin during locomotion in fishes: kinematics, flow visualization, and evolutionary patterns. *Am. Zool.* **40**, 101-122.
Lauder, G. V. (2006). Locomotion. In *The Physiology of Fishes*, 3rd edn (ed. D. H. Evans and J. B. Claiborne), pp. 3-46. Boca Raton, FL: CRC Press.
Lauder, G. V., Madden, P. G. A., Mittal, R., Dong, H. and Bozkurttas, M. (2006). Locomotion with flexible propulsors: I. Experimental analysis of pectoral fin swimming in sunfish. *Bioinspiration. Biomim.* **1**, S25-S34.
Maia, A. and Wilga, C. D. (2013a). Anatomy and muscle activity of the dorsal fins in bamboo sharks and spiny dogfish during turning maneuvers. *J. Morphol.* **274**, 1288-1298.
Maia, A. and Wilga, C. D. (2013b). Function of dorsal fins in bamboo shark during steady swimming. *Zoology* **116**, 224-231.
Maia, A. and Wilga, C. D. (2016). Dorsal fin function in spiny dogfish during steady swimming. *J. Zool. Lond.* **298**, 139-149.
Maia, A., Wilga, C. D. and Lauder, G. V. (2012). Biomechanics of locomotion in sharks, rays and chimeras. In *Biology of Sharks and Their Relatives*, 2nd edn (ed. J. C. Carrier, J. A. Musick and M. R. Heithaus), pp. 125-151. Boca Raton: CRC Press.
Müller, U. K., van den Heuvel, B.-L. E., Stamhuis, E. J. and Videler, J. J. (1997). Fish foot prints: morphology and energetics of the wake behind a continuously swimming mullet (*Chelon labrosus* Risso). *J. Exp. Biol.* **200**, 2893-2906.
Nauwelaerts, S., Wilga, C., Sanford, C. P. and Lauder, G. V. (2007). Hydrodynamics of prey capture in sharks: effects of substrate. *J. Roy. Soc. Inter.* **4**, 341-345.
Quinn, D. B., Lauder, G. V. and Smits, A. J. (2014). Flexible propulsors in ground effect. *Bioinsp. Biomimet.* **9**, 1-9.
Shelton, R. M., Thornycroft, P. J. M. and Lauder, G. V. (2014). Undulatory locomotion of flexible foils as biomimetic models for understanding fish propulsion. *J. Exp. Biol.* **217**, 2110-2120.
Shirai, S. (1996). Phylogenetic interrelationships of Neoselachians (Chondrichthyes: Euselachii). In *Interrelationships of Fishes* (ed. M. L. J. Stiassny, L. R. Parenti and G. D. Johnson), pp. 9-34. California: Academic Press.
Standen, E. M. (2010). Muscle activity and hydrodynamic function of pelvic fins in trout (*Oncorhynchus mykiss*). *J. Exp. Biol.* **213**, 831-841.
Standen, E. M. and Lauder, G. V. (2005). Dorsal and anal fin function in bluegill sunfish *Lepomis macrochirus*: three-dimensional kinematics during propulsion and maneuvering. *J. Exp. Biol.* **208**, 2753-2763.
Standen, E. M. and Lauder, G. V. (2007). Hydrodynamic function of dorsal and anal fins in brook trout (*Salvelinus fontinalis*). *J. Exp. Biol.* **210**, 325-339.
Thomson, K. S. and Simanek, D. E. (1977). Body form and locomotion in sharks. *Am. Zool.* **17**, 343-354.
Tytell, E. D. (2006). Median fin function in bluegill sunfish *Lepomis macrochirus*: streamwise vortex structure during steady swimming. *J. Exp. Biol.* **209**, 1516-1534.
Tytell, E. D. and Lauder, G. V. (2004). The hydrodynamics of eel swimming. I. Wake structure. *J. Exp. Biol.* **207**, 1825-1841.
Wilga, C. D. and Lauder, G. V. (2000). Three-dimensional kinematics and wake structure of the pectoral fins during locomotion in the leopard shark, *Triakis semifasciata*. *J. Exp. Biol.* **203**, 2261-2278.
Wilga, C. D. and Lauder, G. V. (2001). Fluid dynamics and pectoral fin function in the bamboo shark, *Chiloscyllium plagiosum*. *J. Morph.* **249**, 195-209.
Wilga, C. D. and Lauder, G. V. (2004a). Hydrodynamic function of the shark's tail. *Nature* **430**, 850.
Wilga, C. D. and Lauder, G. V. (2004b). Locomotion in sharks, skates and rays. In *Biology of Sharks and their Relatives* (ed. J. C. Carrier, J. Musick and M. Heithaus), pp. 139-164. Boca Raton: CRC Press.
Willert, C. E. and Gharib, M. (1991). Digital particle image velocimetry. *Exp. Fluids* **10**, 181-193.
Zar, J. H. (2009). *Biostatistical Analysis*, 5th edn. New Jersey: Prentice Hall.